

THE TAXONOMY AND MORPHOLOGY OF *PUPPIGERUS CAMPERI* (GRAY), AN EOCENE SEA-TURTLE FROM NORTHERN EUROPE

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SYNOPSIS

Comparative studies show that the chelonians *Eochelys longiceps* (Owen), *Lytoloma trigoniceps* (Owen) and *Lytoloma camperi* (Gray) are conspecific; the valid name is *Puppigerus camperi*, and a lectotype is designated. The species occurs in the Eocene of Belgium and England. All known skeletal elements are described, certain ontogenetic trends are described and discussed, and a few comments are made on the biology.

INTRODUCTION

IN THE collections of many Northern European museums are excellent examples of the cheloniids *Eochelys longiceps* (Owen), *Lytoloma trigoniceps* (Owen) and *Lytoloma camperi* (Gray). All three species are of Eocene age; *E. longiceps* occurs in the London Clay and Bracklesham Beds, *L. trigoniceps* in the Brackleshams only, and *L. camperi* in the Bruxellian of Belgium.

The history of *L. camperi* began in 1781, when Buc'hoz (dec. 6, pl. 3, cent. 2) figured an unnamed turtle carapace from the Sables de Bruxelles; this specimen was later to become one of the two syntypes of *Emys camperi* Gray (1831, p. 37). The species *Chelone longiceps* and *Chelone trigoniceps* were erected by Owen in 1841 and 1850 respectively. The arguments that raged during this period as to the marine or fresh-water affinities of Eocene turtles concerned (*inter alia*) *C. longiceps* and *C. trigoniceps* but not *E. camperi*, which everyone accepted as a marsh turtle.

Cope (1871) erected the new genus *Puppigerus*, with *C. longiceps* and *C. trigoniceps* among the included species, but he did not designate a type. Lydekker (1889*b*) designated *C. longiceps* as the type-species of *Puppigerus*, and, at the same time, transferred the species to the genus *Lytoloma*. *Lytoloma* had also been erected by Cope, in 1870, and is therefore a year older than *Puppigerus*. Lydekker's synonymy, however, is only subjective; and, in any case, the genus *Lytoloma* should have been ignored, being based on two indeterminate species (Zangerl 1953; Moody 1968).

The same author (Lydekker 1889*a, b*) discussed the morphology of the two British species and decided that both were cheloniid turtles. Dollo (1923) claimed the same for the species *camperi*, which too he referred to *Puppigerus*. The belief in the marine

affinities of all these species has persisted. The species *Lytoloma longiceps* [*Chelone*] was made the type of the new genus *Eochelys* by Moody in 1968, who was then unaware that it was already the type of *Puppigerus* Cope. *Eochelys* thus became an objective junior synonym of *Puppigerus*.

In recent years Dr E. Casier, Dr R. Zangerl and I have worked separately on the morphology and taxonomy of the three species. Drs Zangerl and Casier have recently made their material available to me so that the possibly synonymous species could be compared on a wider basis. There is excellent associated material of *Puppigerus* in the Institut Royal des Sciences Naturelles de Belgique, Brussels. On the other hand, material from English localities in English museums consists mainly of well-preserved but isolated skeletal remains; nevertheless a great deal of preparation and jig-saw type assembly carried out at the British Museum (Natural History) has made it possible to compare the prepared material with the associated remains in Brussels. The evidence undoubtedly indicates that the remains of the three species are identical.

HISTORICAL REVIEW

EMYS CAMPERI Gray

The history of the Eocene turtles under revision began with the illustration of a carapace by Buc'hoz in 1781. The specimen remained unnamed until 1784, when Burtin claimed – obviously incorrectly – that it should be referred to the species *Testudo corticata*, a name applied by Rondelet to the Recent Hawksbill Turtle (*Lepidochelys*). Faujas St Fond (1799) agreed with this but, according to Dollo (1923), stated that the specimen was similar to the Recent Green Turtle (*Chelonia mydas*). Cuvier (1812) also thought it was a sea-turtle but, on reflection, described and figured the carapace as one of the marsh turtles from the 'Environs de Bruxelles' (1824, pl. 15, fig. 16 and pl. 13, fig. 8). Gray (1831) regarded Cuvier's description of the turtles from Brussels as an indication of specific grouping and based a new species *Emys camperi* on the two specimens figured by Cuvier. It is fortunate that these syntypes have since proved conspecific, for Cuvier's illustrations are so inaccurate that they could never be regarded as representative of a single species.

The syntypes of *E. camperi* were separated after 1830; the original carapace illustrated by Buc'hoz remained in Brussels as I.R.S.N.B. 1687/R.4; the other and its counterpart were moved to Ghent to become G.M. 2250 and 2251 respectively. The latter were figured and described by Poelman (1868, figs. 1–2), the description confirming that the specimen had eight costal and nine neural plates. As it has not been confirmed whether the last two specimens are still in existence, the Brussels specimen is here designated as the lectotype of the species *E. camperi*. The belief that *E. camperi* was a marsh turtle persisted until 1923, when Dollo assigned the species to the marine genus *Puppigerus* Cope. Bergounioux (1933) disagreed with Dollo's assignment of *E. camperi* to the genus *Puppigerus* and claimed that the species would be more correctly referred to the American genus *Lytoloma*. He supported Dollo's view, however, that *E. camperi* was a marine turtle. His reconstruction of the animal bore little resemblance to the type material.

CHELONE LONGICEPS Owen

Ten years after Gray's erection of the species *E. camperi* upon the forms figured earlier by Cuvier, Owen (1841) described the species *Chelone longiceps* from the London Clay of the Isle of Sheppey; this form was destined to become the type species of both *Puppigerus* Cope 1871 (see Lydekker 1889b, p. 57) and *Eochelys* Moody 1968. *C. longiceps* was erected on skull and shell material correctly assigned to the one species. However, over the next fifty years there was much discussion of the possible synonymy of *C. longiceps* with *Emys parkinsonii*, a species erected by Gray (1831) on remains figured by Parkinson (1811) and Cuvier (1824) from the Isle of Sheppey.

Poelman (1868) decided that the two were synonymous and that *E. parkinsonii* was the senior name, a lead followed by Winkler (1869). This conspecific evaluation was in part correct, as one of the syntypes of *E. parkinsonii* (Parkinson 1811, fig. 2, pl. 18) was a juvenile of 'longiceps' form, a fact noted by Owen (1842) in his description of *C. longiceps*. Since *C. longiceps* is here considered to be a subjective junior synonym of *E. camperi*, the question arises as to the possible synonymy of *E. camperi* and *E. parkinsonii*. Both are proposed on the same page of the same work (Gray 1831, p. 33), *E. parkinsonii* having line priority. The International Code of Zoological Nomenclature recommends (Recommendation 69B (12)) that the first-mentioned name should be used in such cases, all other things being equal. But all other things are *not* equal. *E. parkinsonii* was based on a series of individuals which do not all belong to the same species and from which no lectotype has been chosen, and to use that name in preference to *E. camperi* for all the material described in the present paper would only add to the confusion. It is therefore clear that the recommendation does not apply in this instance and that the name *E. camperi* should be retained.

The species *C. longiceps* and *C. trigoniceps* were regarded as valid by Lydekker, who assigned them in 1889 to the genus *Lytoloma*; this decision succeeded in stabilizing a synonymy confused by Dollo, who had noted the similarity of the two English species with Belgian forms referred variously to the genera *Pachyrhynchus* Dollo, *Erquelinnesia* Dollo and *Euclastes* Cope between 1886 and 1888. The synonymy of the various chelonians from the London Clay was discussed by Moody (1968), when an account of the taxonomic confusion regarding these specimens was given. As mentioned above, Moody erected the new genus *Eochelys* on the species *longiceps*, unaware that that species was already the valid type of *Puppigerus*.

CHELONE TRIGONICEPS Owen

The synonymy of the species *Chelone trigoniceps* followed similar lines to that of *C. longiceps*, the species being first described by Owen in 1849 and first figured, again by Owen, in Dixon's *Geology of Sussex* (1850, pl. XIII, fig. 4). Lydekker (1889b) assigned the species to the genus *Lytoloma* and this has generally been accepted until now.

Stratigraphical occurrence of *Lytoloma*

Sables de Wemmel	Wemmelian	U. Eocene
Barton Beds	Bartonian	U. Eocene
Sables de Bruxelles	Bruxellian	M. Eocene
Bracklesham Beds	Lutetian	M. Eocene
London Clay	Lower Ypresian	L. Eocene

The European material hitherto referred to *Lytoloma* includes the material housed in the I.R.S.N.B., Brussels, under the names *Lytoloma camperi*, '*L. bruxelliensis*' and '*L. wemelliensis*' and in the British Museum (Natural History) under the names *L. longiceps*, *L. trigoniceps* and *L. crassicostatum* (part). As indicated in the introduction to this paper the three Belgian species, *L. longiceps* and *L. trigoniceps* are doubtless all identical and the number of species in this genus is therefore only two.

The supposed differences between *L. longiceps* and *L. trigoniceps* were that *L. trigoniceps* attained greater size and that its interorbital bar was relatively much wider. The latter 'difference' is without doubt the result of distortion and crushing; simple measurement (Table 1B) shows that the relative width of the interorbital bar is exactly the same in the two forms.

A summary of the measurements and indices recorded from the various species (Tables 1 and 2) confirms the comparative studies undertaken. The tables also show that *L. camperi* and *L. longiceps* are conspecific.

TABLE I

Measurements and indices recorded from skulls now referred to the species *Puppigerus camperi* but formerly variously referred to the species *Lytoloma longiceps* and *L. trigoniceps* as well as to *L. camperi*

A. Distance of internal nares from snout/total length of palate

specimen	distance of internal nares from snout		total length of palate \bar{p} (as %)
	n mm	p mm	
<i>Lytoloma camperi</i>			
I.R.S.N.B. R.19	23	52	44.2
I.R.S.N.B. R.18	28	56	50.0
I.R.S.N.B. R.17	45	87	51.7
I.R.S.N.B. R.16	47	92	51.1
<i>Lytoloma longiceps</i>			
H.M. 297	46	87	52.9
Spec. fig. Owen (1849)	46	86	53.6
B.M.(N.H.) R.2163	50	97*	51.5
<i>Lytoloma trigoniceps</i>			
No measurements available			
Specimen referred by Lydekker (1889b)			
to <i>L. crassicostatum</i>			
B.M.(N.H.) 38954	34	72	47.2

* Estimated.

TABLE 1 (cont.)

B. Width of interorbital bar/length of orbit

specimen	width of	length of orbit	$\frac{i}{o}$ (as %)
	interorbital bar		
	i	o	
	mm	mm	
<i>Lytoloma camperi</i>			
I.R.S.N.B. IG.8402	22	25	84.6
I.R.S.N.B. R.19	16	18	88.8
<i>Lytoloma longiceps</i>			
B.M.(N.H.) R.2613	25	27.5	90.9
B.M.(N.H.) 38954	24	26.5	90.6
<i>Lytoloma trigoniceps</i>			
B.M.(N.H.) 39771	29	32	90.6

TABLE 2

Measurements (in mm) and indices recorded from shells now referred to the species

Puppigerus camperi

specimen	Neural plate								
	1st	2nd	3rd	4th	5th	6th	7th	8th	9th
<i>L. camperi</i>									
I.R.S.N.B. IG.9544	33	30	33	33	28	28	22.5	18	9
I.R.S.N.B. R.13	34	30	29	29	24	24	21	15	15
I.R.S.N.B. IG.8632	17	17	15	18	14	12	11	8	5
I.R.S.N.B. IG.8402/R.17	32	29	31	—	—	—	—	—	—
I.R.S.N.B. R.14	—	—	28	30	23	26	21	13	11
<i>L. longiceps</i>									
B.M.(N.H.) 38951	24	26	24	25	23	21.5	19.5	17	—
B.M.(N.H.) 38950	22	17.5	19	20	17	17	16	13	—

Neural shield measurements

specimen	2nd		3rd		4th	
	L	W	L	W	L	W
	<i>L. camperi</i>					
I.R.S.N.B. IG.9544	69	72	65	71	75	65
I.R.S.N.B. R.13	62	68	58	62	61	61
I.R.S.N.B. IG.8632	34	49	34	51	34	45
I.R.S.N.B. IG.8402/R.17	66	72	—	—	—	—
<i>L. longiceps</i>						
B.M.(N.H.) 38951	52	62	50	63	58	56
B.M.(N.H.) 38950	44	56	41	51.5	45	48

Plastral index A

specimen	axillo-inguinal	$\frac{1}{2}$ width of	$\frac{a}{w}$ (as %)
	width		
	a	w	
<i>L. camperi</i>			
I.R.S.N.B. R.14	87	105	82.9
I.R.S.N.B. R.15	92	104	88.5
<i>L. longiceps</i>			
B.M.(N.H.) 45902	52	74	70 ±
B.M.(N.H.) 35721	64	80	80
B.M.(N.H.) 38951	70	95	73.6

TABLE 2 (cont.)

Plastral index B			
specimen	axillo-inguinal width <i>a</i>	length from hypo- hyosuture to xiphi tip <i>h</i>	$\frac{a}{h}$ (as %)
<i>L. camperi</i>			
I.R.S.N.B. R.15	92	136	67.6
I.R.S.N.B. R.14	87	114	76.3
<i>L. longiceps</i>			
B.M.(N.H.) 38951	70	99	70.7
B.M.(N.H.) 25608	53	71	75.7
B.M.(N.H.) 38950	55	73*	75.3
B.M.(N.H.) R.1917	43	64	67.2
B.M.(N.H.) 35721	61	89	68.5
Xiphiplastral index			
specimen	length of xiphiplastron <i>x</i>	length of plastron <i>l</i>	$\frac{x}{l}$ (as %)
<i>L. camperi</i>			
I.R.S.N.B. R.15	87	266	32.7
I.R.S.N.B. R.14	73	218	33.5
<i>L. longiceps</i>			
B.M.(N.H.) 38951	64	201	31.8
B.M.(N.H.) 25608	45	138	32.6
B.M.(N.H.) 35721	54	185	29.2
B.M.(N.H.) R.3964	48	156	30.7
<i>L. camperi</i>			
I R.S.N.B. IG.8632	40	127	31.5

*Estimated.

The obvious synonymy between *L. camperi* and *L. longiceps* is shown by a comparison of the skull I.R.S.N.B. IG.8402/R.17 (Figs. 2-5, Pl. 2) with either the type skull of *C. longiceps* figured by Owen (1849), which is missing presumed lost, or the skull H.M.297, also figured by Owen in 1849. Other comparisons can be made between shell and limb remains, and the similarity is confirmed by a comparison of the plastra of I.R.S.N.B. IG.8632 and B.M.(N.H.) 38951 (Pl. 8).

The belief that the three forms are conspecific renders it necessary to comment briefly on the synonymy. As mentioned above, the species *longiceps* was made the type of the new genus *Eochelys* by Moody (1968), who thought that the generic names *Lytoloma* and *Puppigerus* were both unsuitable. But the realization that *Puppigerus* is an objective senior synonym of *Eochelys*, and the placing of *camperi* and *longiceps* in subjective synonymy, together necessitate that all this material should now be called *Puppigerus camperi*.

This species is described in detail below.

A comparative table (p. 162) of the families Plesiochelyidae, Thalassemydidae, Toxochelyidae and Cheloniidae shows that *Puppigerus* is *not* a thalassemydid, as had been suggested by Cuvier (1824, writing about the material on which Gray later based *E. camperi*). Rather does it confirm Moody's belief (1968) that *Puppigerus* [*Eochelys*] is a cheloniid. In the same work Moody indicated that most British Eocene marine turtles were not toxochelyids.

SYSTEMATIC DESCRIPTION

Family CHELONIIDAE

Subfamily EOCHELYINAE Moody 1968

EMENDED DIAGNOSIS. Skull more or less triangular as seen from above ; dermal and epidermal elements few and regularly arranged (like Cheloniinae, unlike Caretinae). External naris faces forwards and/or upwards ; orbit faces slightly forwards and outwards, with frontal forming part of its rim. Secondary palate may be present, bounded by low, steep cutting edges ; position of internal naris extremely variable. Cervical vertebrae short and stout, articulating as in Recent members of the family. Limbs intermediate in structure between toxochelyids and Recent cheloniids, although humeral : femoral ratio is fully cheloniid. Carapace moderately arched, thickness of plates variable ; neurals eight or nine in number and generally unkeeled. Plastron cruciform, variously ossified, epiplastra wedge-shaped or slightly rounded. No sutural contact between carapace and plastron.

Subfamily includes genera *Puppigerus* Cope (objective junior synonym *Eochelys* Moody), *Argillochelys* Lydekker and *Eochelone* Dollo.

Genus *PUPPIGERUS* Cope 1871

TYPE-SPECIES. *Chelone longiceps* Owen 1841 by subsequent designation (Lydekker 1889b).

EMENDED DIAGNOSIS. Snout of moderate length in juveniles but very elongate, pinched and narrow in the adults of certain species. Occipital shield present in epidermal mosaic. Extensive secondary palate, with or without shallow median sulcus, large area occupied by palatine ; premaxilla and vomer narrow and elongate. Internal narial opening narrow or quite large ; area in front of opening flat, without swelling ridges. Ectopterygoid processes fairly small, anterior pterygoid area narrower than in *Argillochelys*. Basioccipital depression shallow and smooth. Mandible with elongate symphysis, more than one-third the length of the mandible itself ; dorsal surface of symphyseal area very flat or gently concave. Vertebral column as in Recent cheloniids. Carapace more rounded than in *Argillochelys* ; eight or nine neural plates, each slightly longer than broad and with antero-lateral facets much shorter than postero-lateral facets ; vertebral scutes almost square ; fontanelles may be present between costal and peripheral plates in adult specimens. Plastron

COMPARATIVE TABLE

	<i>Plesiochelys</i>	<i>Thalassemys</i>	<i>Idiochelys</i>	<i>Toxochelys</i>	<i>Puppigerus</i> [<i>Lyoloma</i>]	<i>Argillochelys</i>	<i>Lepidochelys</i>	<i>Chelonia</i>
secondary palate	absent	absent	absent	absent	present	partially present	present	present
double or plane joints between cervicals 6, 7 and 8	-	-	-	rare	present	present	present	present
fore limb	as in freshwater turtle?	as in freshwater turtle?	as in freshwater turtle?	flipper-like	flipper-like	flipper-like	flipper-like	flipper-like
hind limb	as in freshwater turtle	as in freshwater turtle	as in freshwater turtle	as in freshwater turtle	as in freshwater turtle	as in freshwater turtle	reduced cheloniid type	reduced cheloniid type
general form	rounded or broadly cordiform	rounded or broadly cordiform	rounded or broadly cordiform	circular	broadly cordiform	broadly cordiform	broadly cordiform	broadly cordiform
neural plates	9	9	partly suppressed	9	9	9	fragmented	8
suprasygal plates	-	1	1	2	2	2	2	2
peripheral plates	22	22	22	22	22	22	normally 24	22
costo-peripheral fontanelles	absent	present	present	present	present in juvenile, often absent in adult	present in juvenile, often absent in adult	present	present
sutural attachment to carapace	present	absent	absent	absent	absent	absent	absent	absent
xiphiplastron	large and square	large and square	large and square	elongated, with notched insertion into hypoplastron	shorter, with notched insertion into hypoplastron	elongated, with notched insertion into hypoplastron	elongated, with notched insertion into hypoplastron	elongated, with notched insertion into hypoplastron
width of vertebrals compared with pleurals	much wider	much wider	much wider	much narrower	much narrower	much narrower	much narrower	much narrower
pleurals	4	4	4	4	4	4	normally 5	4
marginals	24	24	24	24	24	24	normally 26	24

SKELTON

CARAPACE

PLASTRON

EPIDERMAL SHIELDS

extensively ossified, with central fontanelle (if present) of variable size ; epiplastra wedge-shaped as in *Eretmochelys* and *Catapleura*, hyo-hypoplastral suture extensive, xiphiplastra short and broad. Texture of bone surface smooth and without pronounced pattern visible in *Argillochelys*.

***Puppigerus camperi* (Gray) [*Emys*]**

- 1784 *Testudo corticata* (Rondelet) Burtin, p. 93, pl. 5.
 1799 'Tortue Franche' (*Chelonia mydas*) Faujas St Fond, p. 60.
 1824 Emydes de Bruxelles : Cuvier, p. 236, pl. 13, fig. 8.
 1824 Emydes de Sheppey : Cuvier, p. 234, pl. 15, fig. 7.
 1831 *Emys camperi* Gray, p. 33. Based upon Cuvier's figures of 1824.
 1831 *Emys parkinsonii* Gray, p. 33.
 1837 *Emys cuvieri* Galeotti, p. 45.
 1841 *Chelone longiceps* Owen, p. 572.
 1842 *Chelone longiceps* Owen : Owen, pp. 162, 172.
 1849 *Chelone longiceps* Owen : Owen & Bell, p. 16, pls. 3-5.
 1849 *Chelone trigoniceps* Owen & Bell, p. 31.
 1849 *Chelone longiceps* Owen : Owen, p. 16, pls. 12-13.
 1849 *Chelone trigoniceps* Owen : Owen, p. 31, pl. 25.
 1849 *Chelone auticeps* Owen, pl. 25.
 1850 *Chelone trigoniceps* Owen : Owen, p. 218, pl. 13.
 1854 *Chelone longiceps* Owen : Owen, p. 72.
 1868 *Emys camperi* Gray : Poelman, p. 105, pls. 1-2.
 1868 *Emys parkinsonii* Gray : Poelman, p. 111, pl. 3.
 1869 *Emys camperi* Gray : Winkler, p. 129, pls. 26-28.
 1869 *Emys parkinsonii* Gray : Winkler, pls. 24, 25.
 1870 *Puppigerus longiceps* (Owen) Cope, p. 235.
 1886 *Pachyrhynchus longiceps* (Owen) Dollo, p. 138.
 1886 *Pachyrhynchus trigoniceps* (Owen) Dollo, p. 138.
 1889b *Lytoloma longiceps* (Owen) Lydekker, p. 57.
 1889b *Lytoloma trigoniceps* (Owen) Lydekker, p. 53.
 1889b *Lytoloma crassicoatum* (Owen) (part) Lydekker.
 1909 *Emys camperi* Dollo, p. 111.
 1923 *Puppigerus camperi* (Gray) Dollo, p. 416.
 1933 *Lytoloma camperi* (Gray) Bergounioux, pp. 1-13, figs. 1-4.
 1968 *Eochelys longiceps* (Owen) Moody, p. 131.

SYNTYPES. I.R.S.N.B. 1687 - Lectotype, designated herewith.

G.M. 2250, 2251 - Paralectotypes. (As yet no confirmation has been received that these specimens, figured by Poelman (1868), are still in Ghent.)

DESCRIPTION OF LECTOTYPE, I.R.S.N.B. 1687 (Fig. 1). Incomplete carapace, lacking most of the peripheral plates ; specimen very fragmentary on left-hand side ; nuchal incomplete ; nine neural and eight costal plates. On list of types housed in I.R.S.N.B. It is, without doubt, closer to the specimen figured by Cuvier (pl. 13, fig. 8) than the other syntype and is therefore designated herewith as the lectotype of *Puppigerus camperi*.

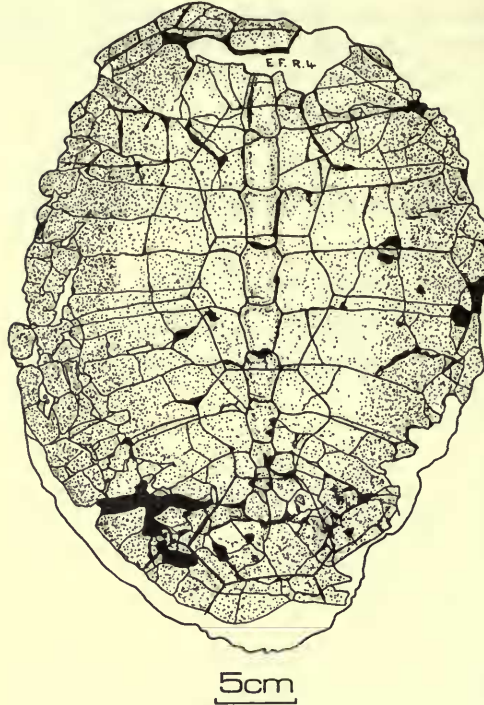


FIG. 1. *Puppigerus camperi* (Gray). Lectotype (I.R.S.N.B. 1687/R.4). From above, drawn from a photograph.

REFERRED SPECIMENS.

- I.R.S.N.B. 1663, 1664, 1665, 1666, 1667, 1668, 1669, 1684, 1685, 1686, 1687/R.4, 1689, R.5, R.13, R.14, R.16, IG.8402/R.17, R.18, R.19
 G.M. 2250, 2251, 2252
 B.M.(N.H.) 25609, 28853, 30526, 35608, 35689, 37207, 37211, 38950, 38954, 38959, 39763, 39771, 44092, R.1025, R.1425, R.1475, R.1481, R.2163, R.8553
 G.S.M. 57266, 57267, 92297, 92298
 Hunterian Collection, R.C.S. H.M.297
 Sedgwick Museum, Cambridge. C.20924, 20926, 20930, 20933
 Maidstone Museum (M.M.) (G.S.M. TN). 9551, 9552, 9554, 9957

Also belonging to this species are two very poor fragmentary mandibles in the I.R.S.N.B. labelled, in Dollo's handwriting, '*Lytoloma bruxelliensis*' and '*Lytoloma wemelliensis*'. These are presumably the specimens upon which, in 1909, Dollo based those two names (they should in fact have been *L. bruxelliense* and *L. wemelliense*, the Greek noun $\lambda\omega\mu\alpha$ being of the neuter gender). The names, however, were given without adequate indication and are certainly *nomina nuda*; since they cannot be formally connected with the specimens they are not included in the synonymy.

OCCURRENCE OF SPECIES.

Sables de Wemmel – Wemmelian – Upper Eocene. Belgium. (See Curry 1966.)
Sables de Bruxelles – Bruxellian – Middle Eocene. Belgium.
Bracklesham Beds – Lutetian to Auversian – Middle Eocene. England.
London Clay – Lower Ypresian – Lower Eocene. England.

The specimens referred to this species range widely in both size and state of preservation. The material studied includes numerous skulls, vertebrae, limb and girdle elements and shells, together with a few excellent associated skeletons (Pl. 1). The smallest known specimens are G.S.M. 57266 and B.M.(N.H.) 28853, of which the last has been prepared with the air-abrasive and has yielded a tremendous amount of skeletal material. The largest specimens are housed in the Belgian collections and reach a maximum length of $350 \pm$ mm. From such a range of material the following specific diagnosis is drawn.

EMENDED DIAGNOSIS OF *P. camperi*. Snout region elongate in adult, tapering anteriorly to a point; in side-view, premaxilla plus maxilla much longer than jugal plus quadrato-jugal. Extensive secondary palate, with narrow internal narial opening situated (in adult) in third quarter of ventral skull length; very long vomer and premaxilla and short rounded palatine; palatal surface pitted. Palatine extends backwards to form a shelf lying ventral to the pterygoid and small ectopterygoid process; pterygoid bar narrow. Basioccipital depression fairly deep, without rugose surface. Braincase basically cheloniid, but with distinct specific characters (see description). Carapace of adult completely ossified, broadly cordiform and gently arched; nine neurals and two pygals; juvenile forms with costo-peripheral fontanelles. Plastron with small to medium-sized central fontanelle; epiplastra wedge-shaped as in *Catapleura*; entoplastron T-shaped; xiphiplastron short and wide. Plastral index 70–85.

DESCRIPTION OF MATERIAL. There are many excellent skulls amongst the specimens listed above, and the following description is drawn from I.R.S.N.B. R.14, R.15, R.16, IG.8402/R.17, R.18 & R.19; B.M.(N.H.) 38954 & R.2613; and H.M.297. The previously noted similarity between the adult skulls formerly ascribed to the respective species *Emys camperi* (Pl. 2) and *Chelone longiceps* (H.M.297), is also apparent in the juvenile specimens I.R.S.N.B. R.19 (Pl. 3A) and B.M.(N.H.) R.1475, in which the snout region is much shorter. The progressive pinching in of the snout as seen in dorsal view is an outstanding ontogenetic trend. The snout of the juvenile is very similar in shape to that of *Chelone crassicostrata*; the snout of the adult, however, is pinched below the orbits and tapers anteriorly to a more pronounced and acutely pointed beak, as is shown particularly well in I.R.S.N.B. IG.8402/R.17 (Figs. 2–5). This pinching in of the snout is demonstrated by a growth series of *P. camperi* skulls (R.19, R.18, R.16 – see Plate 3); this same series also shows the progressive increase in the jugal index from 33.3 to 41.2 (Table 3). It is noticeable that despite this gradual increase in the jugal and quadratojugal indices within the *P. camperi* series, the premaxilla-maxillary length is still proportionally much greater than in the other eochelyines.

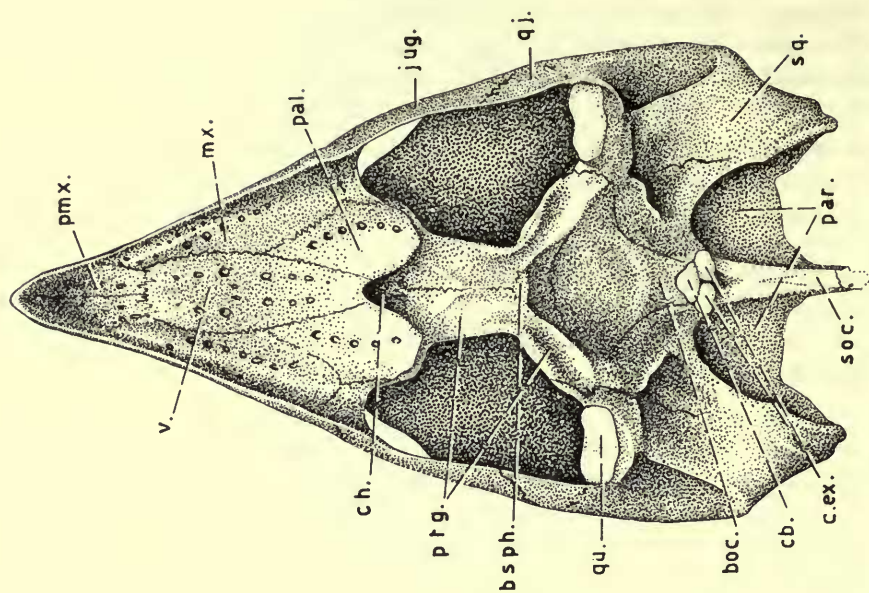


FIG. 3. *Puppiigerus camperi* (Gray). Reconstruction of skull $\times 1$, based on I.R.S.N.B. IG.8402/R.17. From below. Abbreviations as on p. 184.

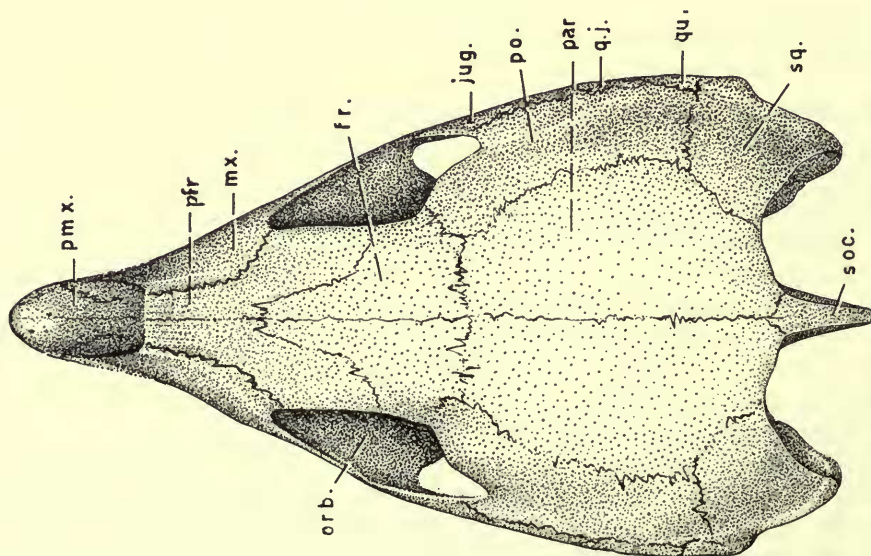


FIG. 2. *Puppiigerus camperi* (Gray). Reconstruction of skull $\times 1$, based on I.R.S.N.B. IG.8402/R.17. From above. Abbreviations as on p. 184.

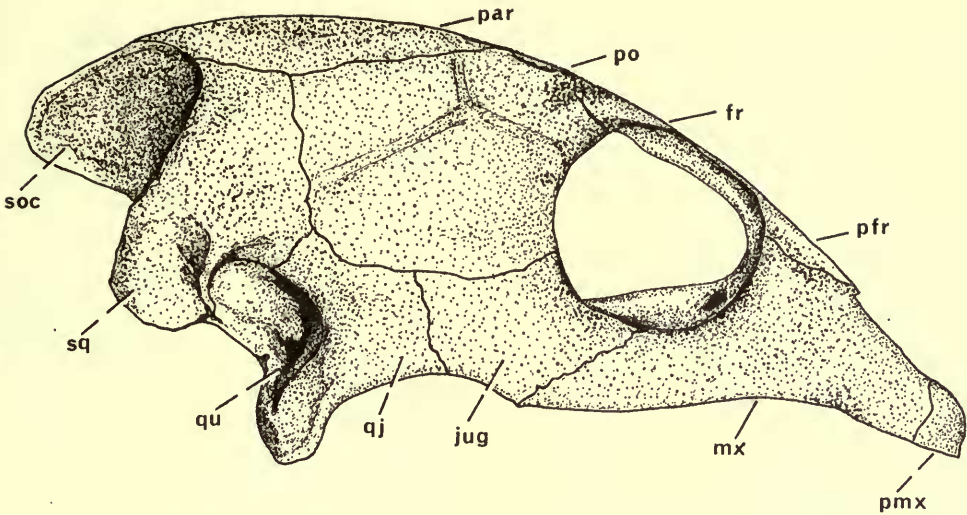


FIG. 4. *Puppigerus camperi* (Gray). Reconstruction of skull $\times 1$, based on I.R.S.N.B. IG.8402/R.17. From right side. Abbreviations as on p. 184.

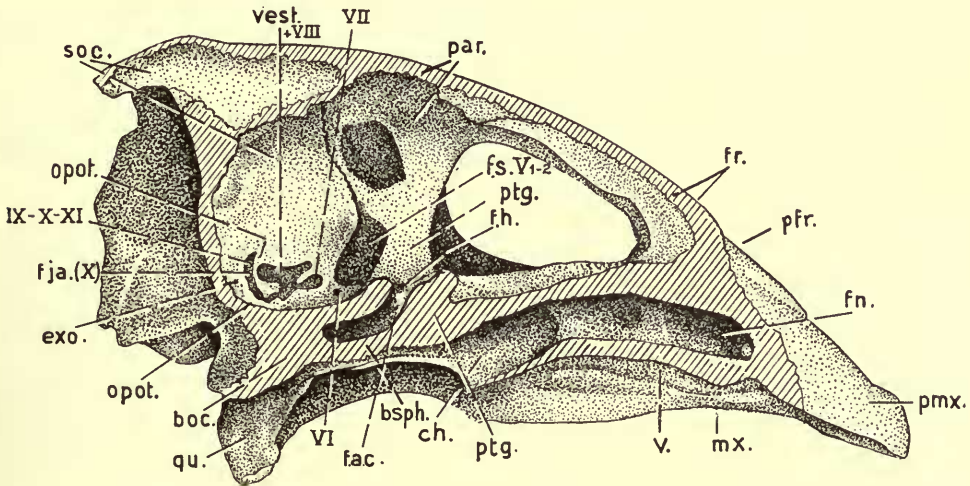


FIG. 5. *Puppigerus camperi* (Gray). Reconstruction of skull $\times 1$, based on I.R.S.N.B. IG.8402/R.17. Parasagittal section close to midline to show braincase. Abbreviations as on p. 184.

Table 4 shows that the internal narial opening is retreating backwards over the ventral surface of the skull as the animal grows. The premaxilla and vomer are elongate in this species, the vomer narrowing anteriorly but expanding slightly in the area of contact with the maxilla and palatine. The palatine is shorter and more rounded than in other species; it often expands medially and posteriorly to reduce the front part of the internal narial opening to a narrow slit (shown well in I.R.S.N.B.

TABLE 3

Measurements (in mm) and indices recorded for the bones of the outside edge of the skulls of three eochelyine species

specimen	total length of premaxilla + maxilla <i>m</i>	length of jugal <i>j</i>	$\frac{j}{m}$ (as %)	length of quadrato- jugal <i>q</i>	$\frac{q}{m}$ (as %)
<i>Puppigerus camperi</i>					
I.R.S.N.B. R.19	27	9	33.3	7	25.9
I.R.S.N.B. R.18	33	11	33.3	5	15.1
I.R.S.N.B. R.17	46	20	43.5	8	17.3
I.R.S.N.B. R.16	51	22	43.1	13	25.5
<i>Puppigerus crassicostratus</i>					
B.M.(N.H.) 37213a	39	23	58.9	8	20.5
B.M.(N.H.) 25610	33	20	60.6	8	24.2
B.M.(N.H.) 35696	32	20	62.5	—	—
B.M.(N.H.) R.3964	—	19	—	7	—
<i>Argillochelys cuneiceps</i>					
B.M.(N.H.) 41636	41	33	80.5	16	39.0

TABLE 4

Measurements (in mm) to illustrate the variation in the position of the internal narial openings with size in *Puppigerus camperi*, and a comparison with other Eocene forms

specimen	length of skull below <i>l</i>	distance of narial opening from tip of snout <i>d</i>	$\frac{d}{l}$ (as %)	quarter in which choanae sited
<i>Puppigerus camperi</i>				
I.R.S.N.B. R.19	52	23	44.2	2
I.R.S.N.B. R.18	56	28	50.0	2-3
B.M.(N.H.) 38954	72	36	50.0	2-3
I.R.S.N.B. IG.8402/R.17	87	45	51.7	3
H.M. 297	87	46	52.9	3
I.R.S.N.B. R.16	92	47	51.1	3
<i>Puppigerus crassicostratus</i>				
B.M.(N.H.) 38955	56	22	39.3	2
B.M.(N.H.) 37213a	64	26	40.6	2
<i>Argillochelys cuneiceps</i>				
B.M.(N.H.) 41636	c. 91	26.5	29.1	1-2

R.16, Fig. 6) and to form a shelf ventral to the ectopterygoid process. The latter is not as pronounced as in either *C. crassicostrata* or *Argillochelys*. The pterygoid bar is narrow in *P. camperi* and does not expand anteriorly to any great extent (Fig. 6). Posteriorly the pterygoid borders the fairly shallow, smooth, basisphenoid/basioccipital depression; the quadrate ramus bears a deep groove running along its ventral surface, its antero-lateral margin curving downwards towards the basioccipital.

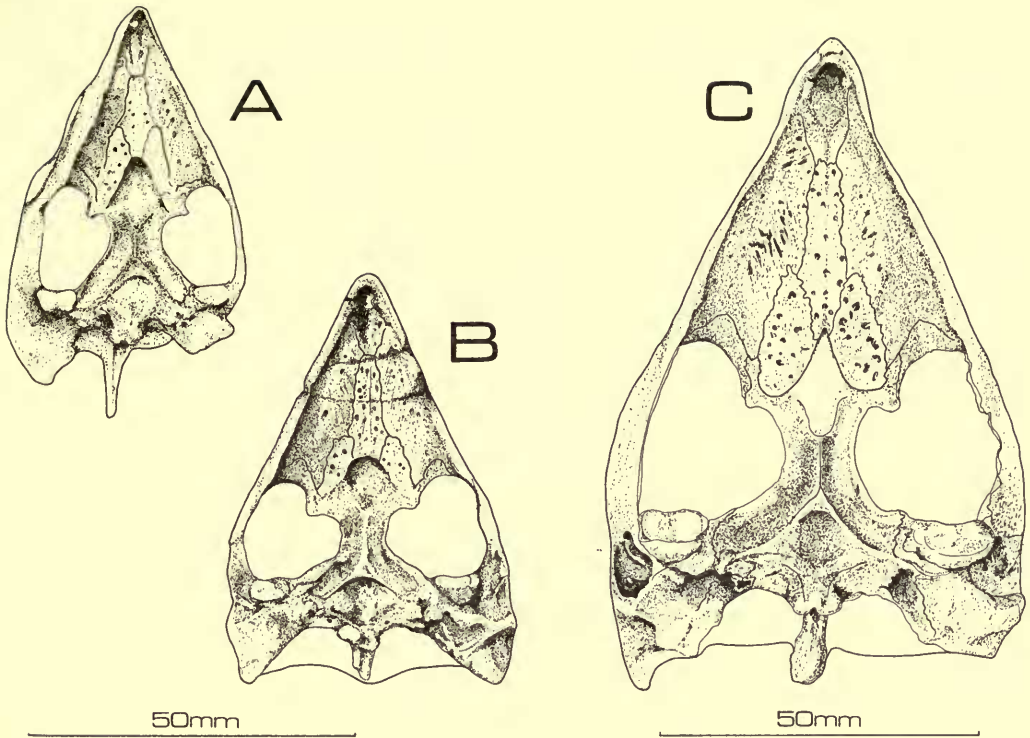


FIG. 6. *Puppigerus camperi* (Gray). Skulls, from below. A. I.R.S.N.B. R.19
 B. I.R.S.N.B. R.18 C. I.R.S.N.B. R.16

Peculiar to the skull I.R.S.N.B. R.19 is the presence of a mid-line foramen, just behind the fronto-parietal suture (Pl. 3A, Fig. 7). This foramen is a definite opening and is not to be confused with the parasitic lesions that so often occur in London Clay specimens. The presence of this parietal foramen was first noted by Edinger (1933) and was later mentioned by Zangerl (1957) in a comparison with *Testudo denticulata*. The foramen is circular and has an anteroposterior diameter of 2.2 mm (Table 5).

TABLE 5

Comparative table

	length of skull mm	distance of parietal foramen from tip of snout mm	diameter of parietal foramen mm
<i>Testudo denticulata</i> R.Z. 612	42	c. 19.5	0.9
<i>Puppigerus camperi</i> I.R.S.N.B. R.19	65 (incomplete)	35	2.2

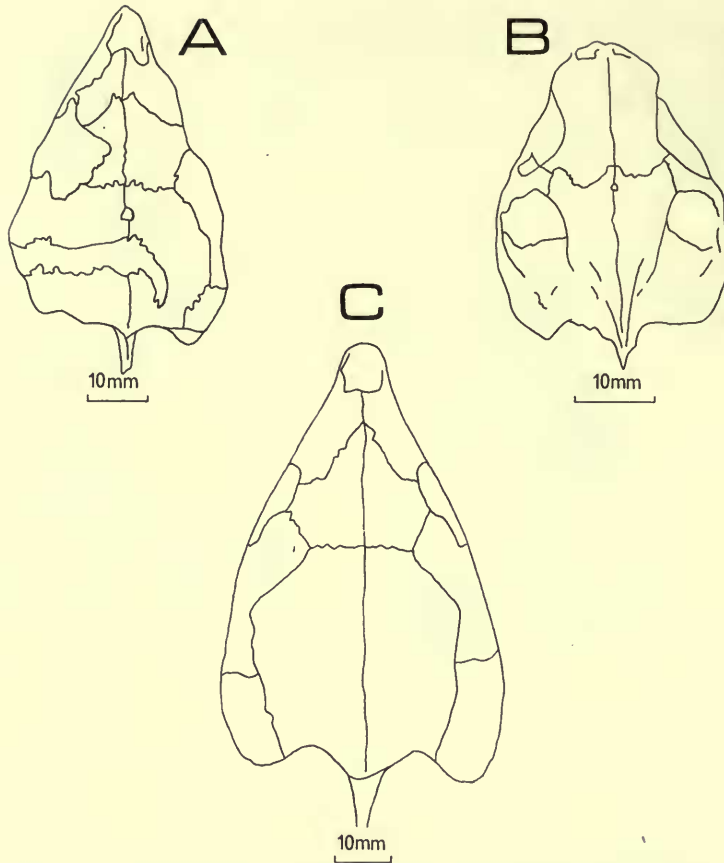


FIG. 7. Reconstructions of skulls of juvenile chelonians, from above, to show parietal foramen. A. *Puppigerus camperi* (based on I.R.S.N.B. R.19). B. *Testudo denticulata* (based on R.Z. 612). C. *Puppigerus camperi* (based on I.R.S.N.B. R.18).

Braincase

The braincase of *P. camperi* is known from the sectioned skull of the Belgian specimen I.R.S.N.B. IG.8402/R.17 (Fig. 5). The bones of the side-wall of the braincase are the pterygoid, parietal, prootic, supraoccipital, opisthotic and exoccipital. The bones of the floor are the basisphenoid, the anterior part of which, the rostrum basisphenoidale, is underlain by the pterygoid, and the basioccipital, which is encroached upon by the exoccipital just anterior to the foramen magnum.

The pterygoid extends upwards from beneath the basisphenoid to form the lower antero-lateral portion of the braincase, the crista pterygoidea. The sulcus cavernosus is well developed between the pterygoid and the rostrum basisphenoidale, much as in *Chelonia mydas*. Postero-laterally the pterygoid forms part of the border of the large foramen nervi trigemini. Laterally the pterygoid is narrower than in most other cheloniids, but not as narrow as in *Argillochelys*. The vertical

pterygoid process fuses with the basisphenoid in the sella turcica region to form a wide shelf in front of and to the side of the dorsum sellae, thus providing a canal between the two bones for the internal carotid. The internal carotid canal therefore joins the sulcus cavernosus well forward of the foramen nervi trigemini; in *Chelonia mydas* the canalis cavernosus is behind this foramen.

Part of the anterior border of the foramen nervi trigemini is formed by the ventral parietal element; the suture between the parietal and the processus pterygoideus beneath it terminates posteriorly at that foramen. In I.R.S.N.B. IG.8402/R.17 the vertical parietal element is apparently pierced by a second large 'foramen' (Fig. 5). This 'foramen' is much reduced on the opposite side of the cavum cranii and, as the bone in that region is translucent in other sectioned skulls, it is probably due to damage and/or subsequent preparation. The vertical prootic component is reduced in lateral view because of the large foramen nervi trigemini anteriorly and the vestibulum posteriorly (Fig. 5); the internal surface area of the prootic is reduced in all eochelyines which have been sectioned, but it is possible that larger specimens were more heavily ossified.

Incomplete ossification may also be an important factor in reducing the internal dimensions of the opisthotic (Fig. 5), which is relatively smaller than in *Chelonia mydas* (Goodrich 1930, fig. 420); it forms an incomplete bar between the vestibulum and the foramen jugulare.

The exoccipital forms the posterior portion of the braincase wall and the posterior border of the foramen jugulare anterius; it is pierced by the foramen for the twelfth nerve.

The dorsal portions of the basisphenoid and basioccipital form the floor of the braincase. The basisphenoid extends anteriorly over the suture of the pterygoid to the posterior area of the palatine; its anterior portion forms the rostrum basisphenoidale, the complete structure of which is unknown because of damage by sectioning. The rostrum appears to have been elongate as in the Cheloniidae but the foramen arteriae cerebialis is much nearer to the dorsum sellae than in Recent forms and is connected ventrally with the pronounced sulcus cavernosus. The sella turcica is overhung by the dorsum sellae. The foramina of the nervus vidianus and nervus abducens are very small, but the processus clinoides is quite large. Behind the dorsum sellae and the processus clinoides the basisphenoid is a concave plate; this plate is divided by a small ridge, the crista basisphenoidalis, which is less pronounced than in the toxochelyids or Recent cheloniids.

The basioccipital too is concave anteriorly, but is encroached upon posteriorly by the exoccipital; only in the toxochelyids does the basioccipital extend backwards dorsally to the occipital condyle. The basis tuberculi basalis and crista basioccipitalis are reduced in *P. camperi*. The basioccipital is smooth on its dorsal surface, the numerous ridges typical of *Toxochelys* and *Chelonia* being absent.

The cavum labyrinthicum and cavum acustico-jugulare of the eochelyines are best known from species other than *P. camperi*. Both are very similar to those of Recent cheloniids and of the genus *Stegochelys* as described by Parsons & Williams (1961 p. 80). This is also true of the columella of *Puppigerus camperi* (known from the specimen B.M.(N.H.) 25599).

Endocranial cast

The endocranial cast (Fig. 8) of *P. camperi* taken from I.R.S.N.B. IG.8402/R.17 reflects very little of the actual brain morphology. The information provided by such casts is of general interest only and, in the main, simply illustrates the principal flexures of the brain (Fig. 8). This lack of detail has been noted previously by Zangerl (1960) and Gaffney (1968). Only in the massively constructed braincase of *Corsochelys haliniches* (Zangerl 1960) are the subdivisions of the brain partially reflected in the endocranial cast.

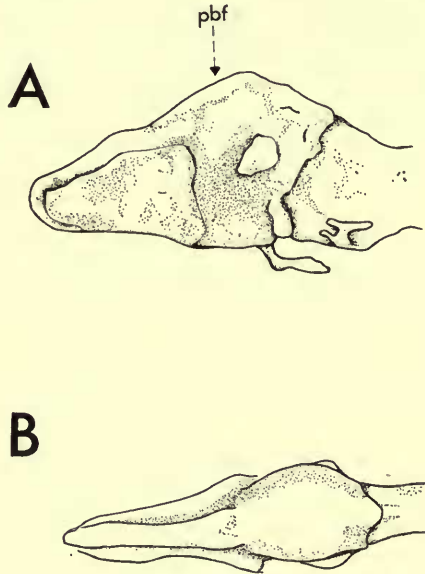


FIG. 8. *Puppigerus camperi* (Gray). Endocranial cast taken from sectioned skull, I.R.S.N.B. IG.8402 $\times \frac{1}{4}$. A. From left side. B. From above. pbf - principal brain flexure.

Lower jaw

The lower jaw of *P. camperi* (Fig. 9; Pl. 2C) is well known from numerous Bruxellian and Bartonian specimens and from one excellent London Clay specimen, B.M.(N.H.) R.8553. The masticatory surface of the jaw is typically almost flat, but does show a very slight concavity in both the anteroposterior and transverse directions. The length of the symphysis is approximately one-half that of the mandibular ramus and the dorsal symphyseal surface is always longer than the ventral. The ventral surface has a faint median ridge and a shallow depression posteriorly. The elongation of the symphyseal region of the lower jaw is a close reflection of the elongate nature of the secondary palate.

Posterior to the mandibular symphyses of specimens I.R.S.N.B. R.15 and I.R.S.N.B. IG.8402/R.17 is evidence of the hyoid apparatus (Fig. 10; Pls. 1 & 2B); in the case of the latter specimen it is to be seen on the nodule bearing the carapace. In IG.8402/R.17 the copula is incompletely ossified and shaped like a tuning-fork;

in R.15 it is more heavily ossified, the body being complete and shield-like in appearance. The first cerato-branchial arches are also present; these are relatively common as skeletal fragments within fossils of this group.

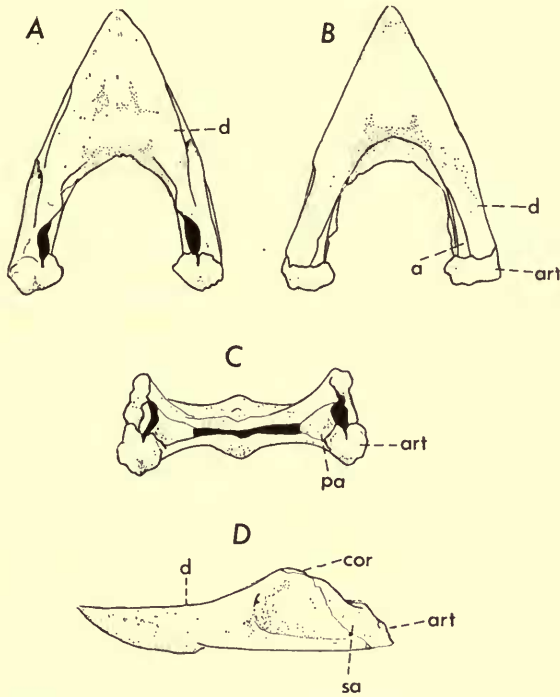


FIG. 9. *Puppigerus camperi* (Gray). Lower jaw $\times \frac{1}{2}$. A. From above. B. From below. C. From behind. D. From left side. Abbreviations as on p. 184.

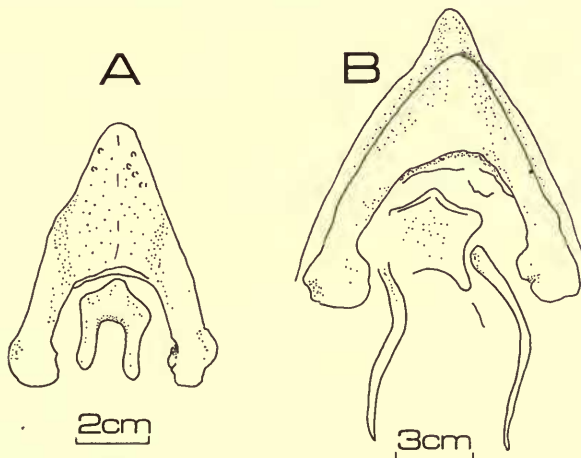


FIG. 10. *Puppigerus camperi* (Gray). Hyoid apparatus. A. Mandible and copula, from below (I.R.S.N.B. IG.8402). B. Mandible, copula and first ceratobranchial arch, from below (I.R.S.N.B. R.15).

Cervical vertebrae

The cervical vertebrae of *P. camperi* are known fully from the prepared specimen B.M.(N.H.) 28853 (Pls. 4-5) and, in lesser degrees, from the specimens I.R.S.N.B. R.14 and R.15; Plates 1 and 6 show the great similarity between the cervical vertebrae of *Puppigerus* and those of *Argillochelys*. As stated previously, they are also very similar to those of all other marine turtles. The immediate difference between the two vertebral series is in the articulation pattern for, whereas that of *P. camperi* B.M.(N.H.) 28853 is (2(3(4)5)6/7)8, that of *Argillochelys cuneiceps* S.M.C. 20937 is (2(3(4)5)6)7)8). The former pattern is characteristic of the advanced sea-turtles (Williams 1950). Other than this, the main differences between the two series are concerned with the depth of the hypapophysial keels and the position of certain zygapophysial surfaces.

In *P. camperi* the hypapophysial keels are exceptionally well-developed on the first five vertebrae and remain as significant features through to the last (eighth) cervical. In *Argillochelys* the keels are again present but, as in *Corsochelys haliniches* (Zangerl 1960) and *Dermochelys* (Völker 1913, pl. 31), are pronounced developments of only the second, third and fourth cervicals. In *Dermochelys* the keels acted as areas of attachment for sheaths of cartilage, and Zangerl postulated a similar rôle for those of *Corsochelys*. The actual function of the cartilaginous sheaths was unexplained, except that it was to be regarded as an advanced marine specialization; my own investigation into this question has resulted in no firm conclusions.

Variation in the zygapophysial surfaces is evident in the second, third and fourth vertebrae of the two series (Pls. 4 & 6). In *Puppigerus camperi* (Pl. 4) the zygapophysial surfaces are more horizontal than those of *Argillochelys* (Pl. 6). This difference would suggest greater lateral movement within the forward neck region of *P. camperi*, which would certainly agree with the inshore mode of life postulated for this form (Moody 1970). The increased tilt of the surfaces in *Argillochelys* would restrict lateral movement but permit greater vertical movement. Once again comparison is made with the form *Corsochelys haliniches* (Zangerl 1960, pl. 32), in which the surfaces are also tilted vertically. Thus the variations in depth of the hypapophysial keel and in tilt of the zygapophysial surfaces may be specializations related to particular environments and modes of life. The cervicals of *P. camperi* show similarities with *Corsochelys* and *Caretta* (Zangerl 1960, pls. 31-33); the position of the neurocentral suture, however, is more like that of *Corsochelys*.

Dorsal vertebrae

The dorsal vertebrae of *P. camperi* have been prepared, together with the central part of the carapace, from the same specimen B.M.(N.H.) 28853 (Pl. 5). This specimen is a juvenile, so that the dorsal vertebrae are not completely fused together; a ventral view shows large spaces between the first five centra. Spaces are also present between the rib heads and the synapophyses. All these spaces were filled with cartilage during the early stages of growth. Each dorsal vertebra (except the first) is fused to the corresponding neural plate; the first, which lies beneath the nuchal

plate, is somewhat similar to the eighth cervical in that it has a much reduced centrum and an elongate neural arch. The centrum of the first dorsal is procoelous to receive the condyle of the eighth cervical; and the whole vertebra is tilted forwards to an angle of some 45 degrees, the posterior portion of the neural arch touching the ventral surface of the nuchal plate. After the first, the centra of the dorsal vertebrae are much reduced, laterally compressed and constricted in the centre to give a waisted appearance. The ends of the centra of this immature specimen are flat. The dorsal blade formed by the fusion of the neural arches is very thin, although it does expand anteriorly with the rest of each arch to form the dorsal part of the synapophyses; the ventral portions of the latter are formed by the underlying centra. The neural arches are intercentral in position, each being extended forwards; the spinal nerve openings occur above the middle of each centrum. Hoffstetter & Gasc (1969) described the composition of the same region in *Pseudemys ornata*, which appears to be very similar.

The ribs arise intervertebrally, as in all turtles, and they arch upwards to fuse with the carapace. The tunnel formed between the vertebrae, ribs and costal plates is in life occupied by epaxial musculature (Vallois 1922, fig. 16); it is well developed as far back as the third rib, but is then reduced to a very small opening. The first rib is reduced and fused distally with the second (as is typical of sea-turtles). The notch between the articular facets of the two ribs is similar to that of the Cheloniidae.

Sacral and caudal vertebrae

The sacral vertebrae of *P. camperi* are known from the specimen H.M.297; another specimen, B.M.(N.H.) R.1480 (Fig. 11), has similar sacrals but is without a skull and cannot be determined with certainty. The sacrum of the latter specimen is made up of two sacral vertebrae and a modified first caudal, all ankylosed together. The centrum of the first sacral is strongly procoelous whilst the first caudal has a large

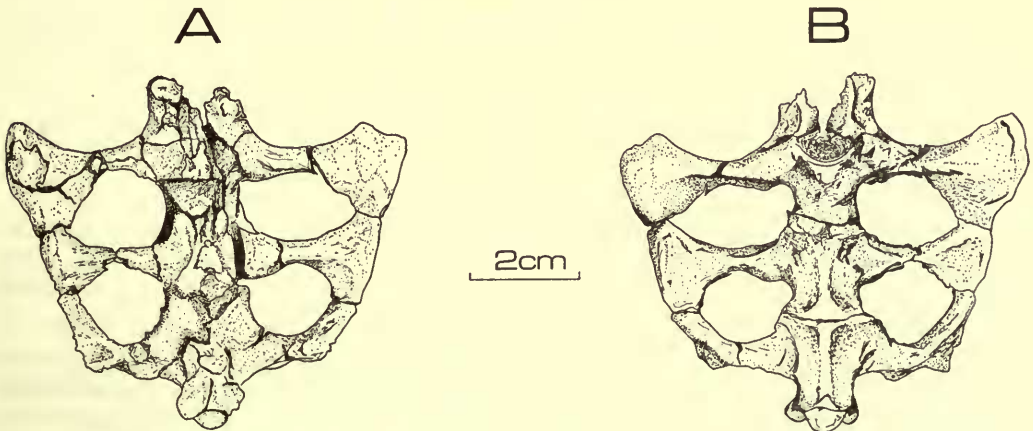


FIG. 11. *Puppigerus camperi* (Gray). Sacrum (B.M.(N.H.) R.1480). Specimen referred by Lydekker to *Lytoloma trigoniceps* (Owen). A. From above. B. From below.

condyle posteriorly; radiography, however, has failed to show whether all these vertebrae are procoelous. Sharp neural crests are visible and the first caudal bears large postzygapophyses. The first sacral rib is greatly expanded laterally and in side-view is thickened anteriorly. The second rib, although smaller, is also expanded. In H.297 the first sacral vertebra and rib are missing, but the other two vertebrae and ribs are very similar to those of B.M.(N.H.) R.1480. In both specimens the caudal rib is expanded anteriorly and curved distally.

Two caudal vertebrae remain attached to the sacrum of H.297, but the only other articulated caudal vertebrae attributable to this species are three vertebrae of specimen I.R.S.N.B. R.14 (Pl. 1A), the centra of which are similar to those of the dorsal vertebrae; they are 22 mm, 16 mm and 13 mm long respectively.

Girdles and limbs

The girdle and limb material prepared from the immature specimen B.M.(N.H.) 28853 (Pl. 5) shows clearly the peculiar mixture of cheloniid and toxochelyid characters noted for the Eochelyinae by Moody (1968). This is shown even better by disarticulated elements referred to mature specimens of the same species.

The pectoral girdle and fore limb definitely tend towards the cheloniid condition. The scapula (Pl. 5C) has a pronounced 'neck region' between the glenoidal and coracoidal facets and the base of the bifurcation, while the coracoid (Pl. 5E) is much longer than the dorsal process of the scapula. A table (Table 6) of the measurements and indices of the shoulder girdle in the Toxochelyidae, Eochelyinae and Recent Cheloniidae shows clearly the direct affinities between the latter two groups.

TABLE 6

Shoulder girdle measurement and indices of the Toxochelyidae, Eochelyinae and Recent Cheloniidae

specimen	V_a	V_b	$\frac{V_b}{V_a}$ (as %)	V_c	$\frac{V_c}{V_a}$ (as %)	V_d	$\frac{V_d}{V_a}$ (as %)
<i>*Toxochelys latimeris</i>							
Y.P.M. 3602	26	13.5	51.9	34.5	132.7	—	—
C.N.H.M. PR.123	940	48.0	51.0	122.0	129.7	137	145.7
<i>Puppigerus camperi</i>							
B.M.(N.H.) 28853	26	15	57.7	29	111.5	41	157.7
<i>*Lepidochelys kempi</i>							
C.N.H.M. 31334	76	25.5	46.7	90	118.4	118	142.5
B.M.(N.H.) 1940.3.13.1	40	18.5	46.2	47	117.5	57	162.5
<i>*Chelonia mydas</i>							
C.N.H.M. 22066	153	89	58.1	183	119.6	304	198.7

V_a = length of ventral prong of scapular fork from tip of process to edge across neck of scapula.

V_b = length of scapular neck from base of fork to ridge dividing glenoidal facet from coracoid suture face.

V_c = length of dorsal prong of scapular fork from tip of process to edge across neck of scapula.

V_d = maximum length of coracoid.

*After Zangerl (1953, tab. 5).

The humerus of *P. camperi* (Pl. 5D) has a straighter shaft than that of the toxochelyids and a more pronounced radial process, which latter is also situated further down the shaft. The humerus is similar to that of *Eochelone brabantica* and other cheloniids such as '*Chelone*' *vanbenedeni* Smets 1886, *Corsochelys haliniches* Zangerl 1960 and *Desmatochelys lowi* (Zangerl & Sloane 1960).

The radius and ulna are known only from a few specimens and are usually un-associated. The two bones lie close to each other in I.R.S.N.B. R.15 (Pl. 1B), and measure 41 mm and 32 mm respectively.

A comparison with the fore limb bones of the Recent Cheloniidae and the Toxochelyidae (Table 7) brings out two interesting points. First, as in the Recent cheloniids, the radius of *Puppigerus* is much larger than the ulna; secondly, those two bones are proportionally shorter in relation to the humerus than those of either the Recent Cheloniidae or the Toxochelyidae.

TABLE 7

Measurements (in mm) and indices of the fore limb bones of the Eochelyinae, Recent Cheloniidae and Toxochelyidae

	length of humerus <i>h</i>	length of radius <i>r</i>	$\frac{r}{h}$ (as %)	length of ulna <i>u</i>	$\frac{u}{h}$ (as %)
EOCHELYINAE					
<i>Puppigerus camperi</i>					
I.R.S.N.B. R.15	74	41	55.4	32	43.2
RECENT CHELONIIDAE					
* <i>Eretmochelys imbricata</i>					
C.N.H.M. 31009 (sub adult)	79	48	60.7	42	53.1
* <i>Chelonia mydas</i>					
C.N.H.M. 22066 (adult)	213	140	65.7	110	51.6
TOXOCHELYIDAE					
* <i>Toxochelys latimeris</i>					
Y.P.M. 3602	37	—	—	—	—
C.N.H.M. PR.123	130	—	—	65	50.0
* <i>Toxochelys moorevillensis</i>					
C.N.H.M. PR.136	± 120	—	—	60	50.0

* After Zangerl (1953, tab. 8, p. 177).

Bones of the pelvic girdle and hind limb are much more commonly preserved than those of the pectoral girdle and fore limb. The bones prepared from B.M.(N.H.) 28853 (Pl. 5) allow a direct statistical comparison to be made with other turtles, and the index of 23.2 recorded for the area of the eochelyine ischium against the area of the pubis falls between the 14.9 and 46.3 recorded for *Eretmochelys* and *Toxochelys* respectively (Table 8). The development of a pronounced posterior spur on the ischium (Pl. 1A; Fig. 12) distinguishes the girdle of this species from those of the Recent Cheloniidae. The general morphology of the pelvic girdle of *P. camperi* is, as in other eochelyines, intermediate between the toxochelyid and cheloniid conditions.

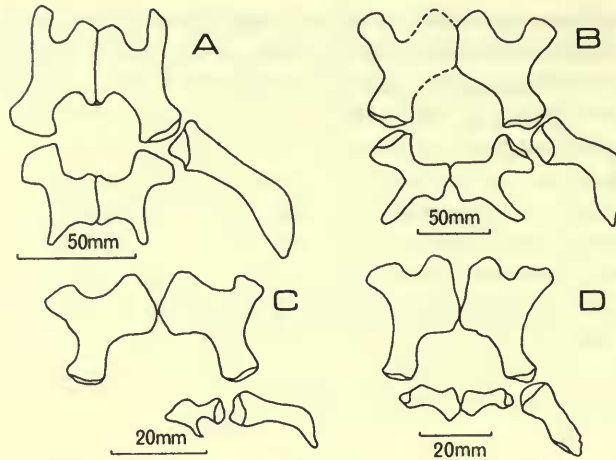


FIG. 12. Chelonian pelvic girdles. A. *Chelydra*. B. *Toxochelys*. C. *Puppigerus*. D. *Eretmochelys*. A, B and D from Zangerl, 1953, p. 163.

TABLE 8

Measurements (in mm²) and indices of surface areas of ischium and pubis in *Eretmochelys*, *Puppigerus* and *Toxochelys*

	area of pubis <i>p</i>	area of ischium <i>i</i>	$\frac{i}{p}$ (as %)
* <i>Eretmochelys imbricata</i> C.N.H.M. 22352	2217	331	14.9
<i>Puppigerus camperi</i> B.M.(N.H.) 28853	2442	566	23.2
* <i>Toxochelys moorevillensis</i> C.N.H.M. P.27391	2308	1069	46.3

* After Zangerl (1953, tab. 6, p. 164).

Several bones of the pelvic girdle and hind limb are present in the specimen I.R.S.N.B. R.15 (Pl. 1B), in which the femur and tibia may be measured and compared with the humerus, radius and ulna (Table 7). The femur is approximately 50 mm in length and, although morphologically identical to that of the *Toxochelyidae*, is shorter in relation to the humerus than that of even the Recent *Cheloniidae*. The index femur/humerus is 67.5, as against 70.9 for *Eretmochelys* and 75.1 for *Chelonia* (see Zangerl 1953, p. 177, tab. 8). The index tibia/humerus is 66.3 and is similar to those recorded for both *Cheloniidae* and *Toxochelyidae*. Partial pelvis and hind limbs from other specimens (I.R.S.N.B. R.14 (Pl. 1A), IG.8632, B.M.(N.H.) 25608 and 38950) show the same characteristics as those described above. The femur/humerus ratio of I.R.S.N.B. IG.8632 is 65.6, as against the 67.5 recorded for the adult specimen I.R.S.N.B. R.15.

R.15 also includes two distal tarsals and all five metatarsals. The bones are very little disturbed and are of similar proportions to the same elements in the hind limb

of modern sea-turtles. Distal tarsal III is rounded and similar to that of the species *Glarichelys knorri* Zangerl (1958). The lengths of metatarsals II-V are 19 mm, 20 mm, 20.5 mm and 15 mm respectively.

Carapace and plastron (Reconstruction Fig. 13)

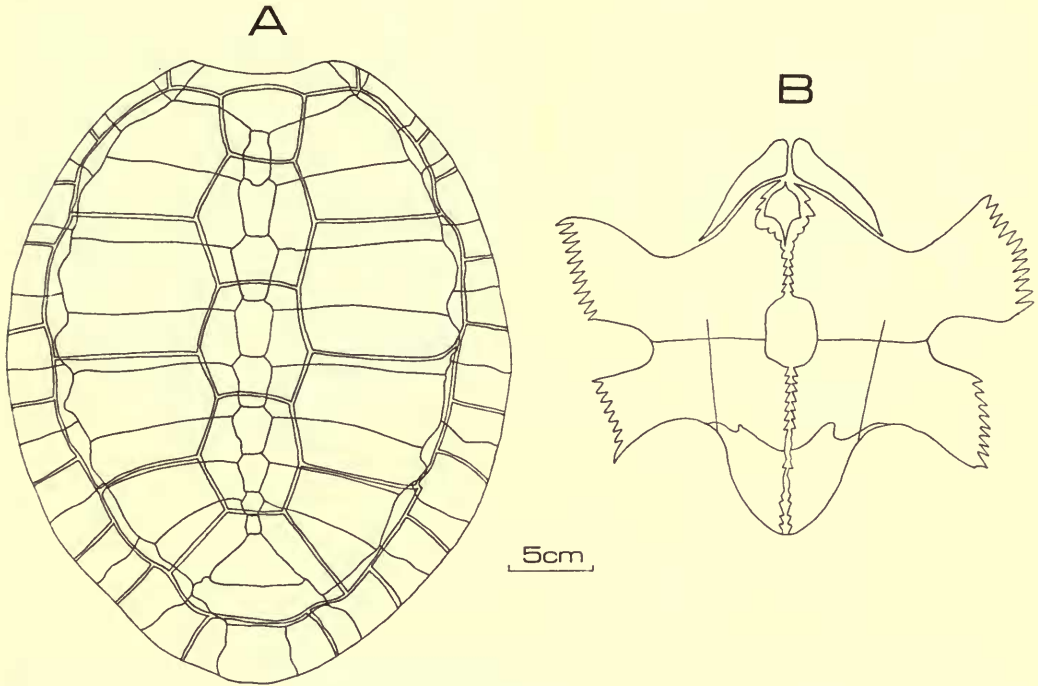


FIG. 13. *Puppigerus camperi* (Gray). Reconstructions of shell.
A. Carapace. B. Plastron.

Several excellent shells of *P. camperi* are housed in the Brussels Institute; they are numbers I.R.S.N.B. R.13, R.14, R.15, IG.8402, IG. 8632, IG.9544, 1666 and the lectotype 1687/R.4. Most of them include remains of both carapace and plastron, so that the task of description is much simpler than it would be if one had to rely solely on British material. Comparative measurements of specimens from both countries are listed in Table 2 to support the subjective synonymy of the species *P. camperi* and *P. longiceps*. Variation in the neural and pygal plates of the several carapaces is only very slight and the pattern of the central dermal plates is characteristically constant; this contrasts with the condition in *Argillochelys antiqua*, where the relationship between the first and second neurals is inconstant and the sizes of the last three extremely variable. In *P. camperi* the first neural is usually biconvex and the last three neurals always become progressively shorter. A comparison with other eochelyines emphasizes the invariability of the central dermal plate pattern.

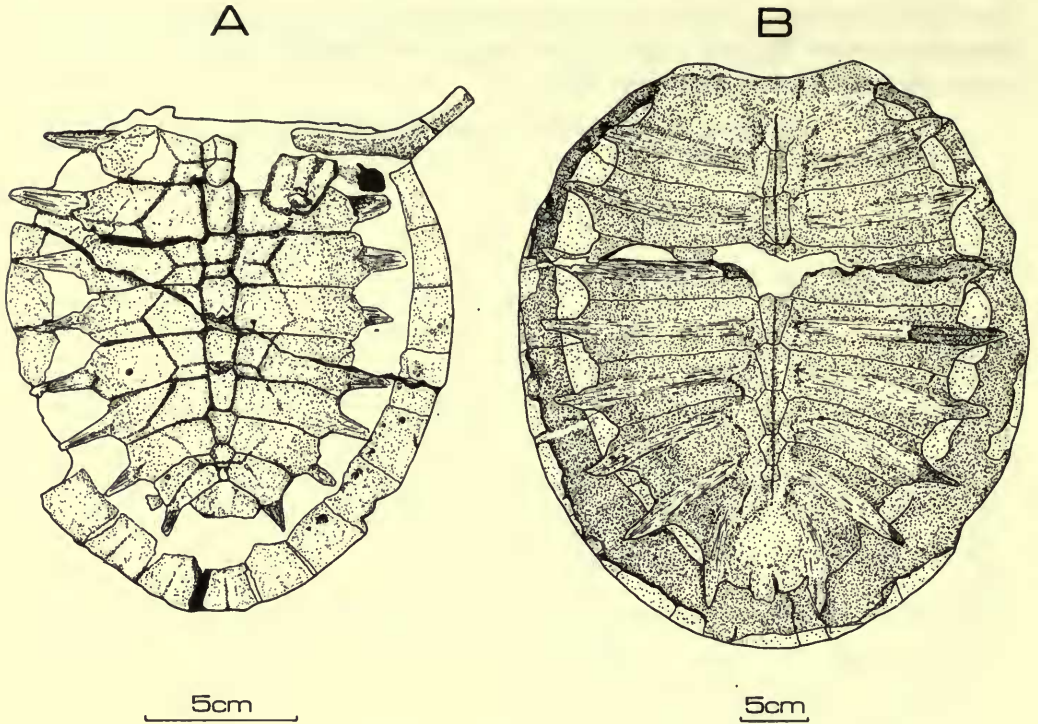


FIG. 14. *Puppigerus camperi* (Gray). Carapaces from above.
A. I.R.S.N.B. IG.8632. B. I.R.S.N.B. IG.1663.

In the juvenile specimens I.R.S.N.B. IG.8632 and G.S.M. 57266 the carapace is not completely ossified and large costo-peripheral fontanelles are present along its margin, from the nuchal to the pygal plates. In IG.8632 (Fig. 14A) the second suprapygal is missing, perhaps because of imperfect preservation. As the animal grows the costal and peripheral plates gradually occlude the lateral fontanelles (Fig. 15); the carapace of the adult is completely ossified, e.g. in I.R.S.N.B. IG.9544 (Pl. 7B). This closure of the lateral fontanelles occurs only in *Puppigerus* and, in consequence, the peripheral plates of that genus are larger than those of related forms. Another change in the development of the carapace is seen in the lengthening and rounding of the epidermal scutes in the adults, for those of the juveniles are relatively broader and much more angular (Fig. 15). In specimen IG.9554 the outlines of the vertebral scutes are double and indicate successive growth stages (Pl. 7B). The ontogenetic changes described above for the Belgian specimens are also visible in certain British carapaces, which range from the very well-preserved juvenile G.M. 57266 to the large adult B.M.(N.H.) 38951.

All the British specimens are incomplete; the main casualties are the peripheral plates, which are known from very few specimens indeed. But, in spite of these preservational defects, the carapaces of *P. camperi* can be easily recognized through the description given above and by the constancy of the plate pattern.

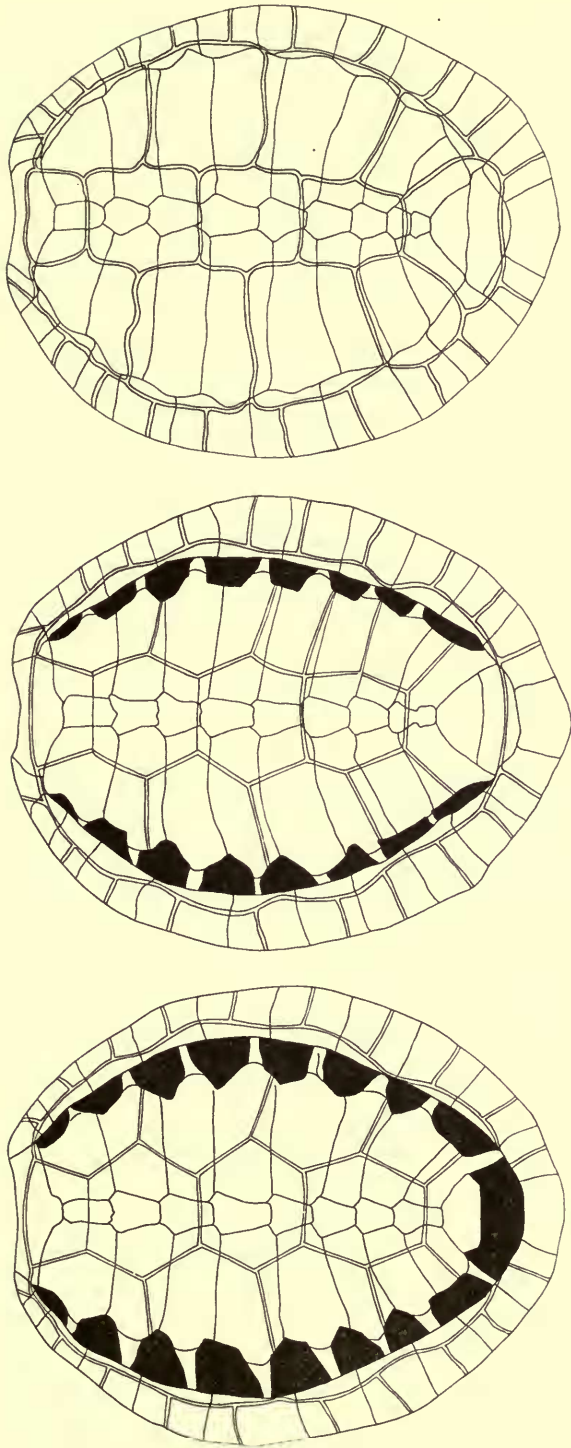


FIG. 15. *Puppigerus camperi* (Gray).
Growth series of carapaces (not to scale) to show increased ossification during ontogeny.

The plastra of the two Belgian specimens I.R.S.N.B. R.14 and R.15 (Pl. 1) are, without doubt, the best examples of the ventral shell of *P. camperi*. Both have all their plates and in R.15 each plate is in its correct position. The epiplastra are shown beautifully in the latter specimen and are typically wedge-shaped, like those of the genus *Catapleura* (Schmidt 1944). The xiphiplastra are shorter and broader than those of *Argillochelys*, sutural contact existing along their whole length, and their notched contact with the hypoplastra is less acute. The difference between the notched contacts of *P. camperi* and those of *Eochelone brabantica* is even more pronounced. The specimens I.R.S.N.B. IG.8632 (Pl. 8A), IG.8402 (individual plates), and B.M.(N.H.) 25608, 28853, 38950 and 38951 (Pl. 8B) also illustrate the form of the plastron in *P. camperi*.

The central fontanelle, which Cuvier (1824) used as one of the characters justifying his association of this form with the 'émydes', is a consistent feature throughout the ontogeny of *P. camperi* (Pl. 8). In forms such as *Lepidochelys olivacea olivacea*, however (see Zangerl 1958, Abb. 27), this fontanelle varies greatly in size.

The plastral indices recorded for *P. camperi* show a high intraspecific variability, with a range of 70-90 for plastral index A and of 65-75 for plastral index B (Table 2). It is therefore recommended that isolated plastral material should be identified not only on these indices but also on other proportional differences, including the slight variation in xiphiplastral lengths of the three genera *Argillochelys*, *Eochelone* and *Puppigerus*.

The terminology of the various shell elements is explained by Zangerl (1969).

SUMMARY AND CONCLUSIONS

The account given represents a taxonomic and morphological study of all available material hitherto referred to the species *Lytoloma camperi*, *L. longiceps* and *L. trigoniceps* of Belgium and England. All this material is recognized as conspecific, the rules of priority requiring that the species be called *Puppigerus camperi*.

The morphology of this species is mainly cheloniid but the pelvic girdle and hind limb retain several primitive characters. The functional purpose of a combination of cheloniid fore limb and toxochelyid hind limb was probably to enable alternate slow cruising and rapid paddling (Zangerl 1953). Although this type of movement is postulated for this species and many others of similar morphology, no light is thrown on to the habitat or feeding habits of the animal. The jaws of *P. camperi* are characteristic elements but they too give little information as to the likely feeding habits. Dollo (1909) stated that *Lytoloma bruxelliensis* fed on oysters but, although the feeding habits of turtles are in some species restricted to particular diets, they generally vary according to the availability of food.

In *Chelydra serpentina*, the Recent snapping turtle, the form of the jaw suggests a diet consisting exclusively of fish or other animals; this, however, is not so, for the turtle is known to consume large quantities of vegetable material (Lagler 1943). Nor is a secondary palate an invariable indicator of a durophagous diet, for it occurs in plant-eaters such as *Chelonia mydas*.

The sediments in which *P. camperi* is found contain great quantities of vertebrate and invertebrate material and, in the case of the London Clay, an abundance of plant

material too. The size of the secondary palate varies considerably in the Eochelyinae and this suggests a variation in diets, but as yet no one knows what *P. camperi* fed on.

The limb pattern and the suggested type of locomotion would tend to indicate a wider variety of ecological niches in the Eochelyinae than is found in freshwater forms. It is probable that the eochelyines dwelt mainly on the coast and in coastal inlets but could also travel into the open sea.

As in the toxochelyid turtles described by Zangerl (1953), parasitic lesions are very common. Some of the specimens are badly affected, with infestations occurring mainly on the shell plates but also on the skulls. The skull infestations sometimes penetrate the bone and may have been the cause of death. Thicker bone often surrounds the cavities caused by the parasites.

Most of the London Clay and Bartonian specimens are disarticulated and incomplete, but some specimens do retain attached skulls or limb fragments, indicating that scavenging and current action were not severe.

Specimens are more frequently damaged (crushed and distorted) by post-depositional compaction and are often destroyed by pyritization. The Belgian material occurs in a sandstone and is often complete in its preservation; this suggests very peaceful burial conditions.

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ABBREVIATIONS

The names of Museum and other collections have been abbreviated as follows:

B.M.(N.H.)	British Museum (Natural History), London
C.N.H.M.	Field Museum of Natural History, Chicago
G.M.	Geological Museum, Institute of Geological Sciences, London
H.M.	Hunterian Museum, Royal College of Surgeons, London
I.R.S.N.B.	Institut Royal des Sciences Naturelles de Belgique, Brussels
M.M.	Maidstone Museum
R.Z.	Rainer Zangerl's private collection
S.M.C.	Sedgwick Museum, Cambridge
Y.P.M.	Peabody Museum of Natural History, Yale University, New Haven

Other abbreviations

a	os angulare	mx	os maxillare
art	os articulare	opot	os opisthoticum
boc	os basioccipitale	orb	orbit
bsph	os basisphenoideum	p	pubis
cb	condylus basioccipitalis	pa	os praearticulare
cex	condylus exoccipitalis	pal	os palatinum
ch	internal narial opening	par	os parietale
cor	os coronoidum	pbf	first principal brain flexure
d	os dentale	pfr	os prefrontale
exo	os exoccipitale	pmx	os premaxillare
fac	foramen arteriae cerebralis	po	os postorbitale
fh	fossa hypophyeos	ptg	os pterygoideum
fja	foramen jugulare	qj	os quadrato-jugale
fn	foramen nasale internum	qu	os quadratum
fr	os frontale	sa	os surangulare
fs	foramen nervi trigemini	sq	squamosal
i	ilium	soc	os supraoccipitale
is	ischium	v	vomer
jug	os jugale	vest	vestibule

Cranial nerves

v	trigeminal	ix	glossopharyngeal
vii	facial	x	} vagus and accessory
viii	acoustic	xi	
		xii	hypoglossal

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